AN APPROACH TO THE PREDICTION OF DECOMPOSITION RATES IN FORESTS THROUGH MOISTURE BUDGETING TECHNIQUES

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If one were to conceptualize the turnover of organic matter by ecosystems in the simplest manner possible, one would probably visualize a cycle. The cycle could be expressed as phases beginning with the production of organic matter, followed by some transient storage, and finally completed with grazing and decomposition of the organic matter originally produced.

In most forests the percentage of organic matter consumed by herbivores is quite small. As suggested by Lindeman the primary agents for breakdown of organic matter are the saprophagous organisms which require as their source of food dead organic molecules (Lindeman, 1942). In forests decomposition is located primarily at the forest floor. Here leaves, twigs and trunks are deposited. The excrement of animals and their dead bodies come to rest on the forest floor where organic molecules are processed and broken into their component parts.

Unlike the warm-blooded animals which can search for food (graze) and maintain a rather high rate of activity in a variety of environments, the decomposer organisms are largely cold-blooded and depend on the quality of the local environment for their reproduction, growth, and metabolism. It is primarily the environment of the decomposers which controls the rate at which organic matter is recycled, and the constituent nutrients are released for reuse by the primary producers.

ENVIRONMENTAL CONTROLS OF DECAY ORGANISMS

In order to accomplish the decompositional breakdown of organic debris it has been verified repeatedly that free film moisture and ambient energy are required. Burges (1965), Greenwood (1961), and Wiant (1967b), as well as many

others, confirm that a free film of water is required for micro-organisms to assimilate oxygen and food. When the water film is insufficient, the process of decomposition will stop. Analysis of data from Wiant (1967b) and Broadfoot and Pierre (1939) indicates furthermore that moisture requirements by the decomposers display a threshold. The rate of decay declines rapidly when the weight of the moisture in the substrate is dried to a little less than 100 percent of the substrate's oven dry weight. But through a large range of moisture values, even in excess of 400 percent, the rate of decay is virtually unchanged.

Similarly, environmental variables such as the temperature of the substrate are often cited as regulators of decomposition rates because microorganisms require a supply of external energy. Available evidence of temperature influences on microorganisms was reviewed by Wiant (1967a). He reports from his own data as well as from others that reactions by microorganisms follow the law of Van't Hoff and Arrhenius at temperatures below 40°C. This law specifies a doubling of chemical activity for each increase in temperature of 10°C. Evidence gathered by Reiners (1968) confirms this relationship for decay organisms down to 0°C.

It is clear that energy and moisture must be present for the decomposers to consume debris such as forest litter. There are, however, other mechanisms which ultimately influence rate of decay. These include the mechanical properties of organic matter, its chemistry, the formation of toxins, and the controls of succession by microorganisms (Burges, 1965). These additional variables may induce feedbacks which result in varying accumulations of organic mass in storage even in places where the energy and moisture endowments are the same. But it is also clear that these mechanisms are not the absolute factors which regulate rates of decomposition. They are modifying mechanisms which may be expressed conveniently in an inhibitory role or as mediators of efficiency of decay organisms. The overriding environmental control of decomposer systems is manifested in the energy and moisture which is endowed to the ground region and allocated among various natural systems including the decomposer environment.

AN HYPOTHESIS

If the decomposer system of the forest floor is activated by ambient energy while adequate moisture is available, as evidence indicates is the case, then the water budget variable, Actual Evapotranspiration, may be a reasonable predictor of the rates of substrate decay. Actual Evapotranspiration is the only climatic variable which rises in value as the energy is available until or unless moisture is in short supply. For example, low rates of Actual Evapotranspiration indicate either a low supply of energy and/or a low supply of moisture. Actual Evapotranspiration is a surrogate of the energy which is effective while moisture is adequate and should therefore serve as an indication of the timing and relative effectiveness of the energy which drives physical and biological processes including the work enacted by decomposer heterotrophs on forest litter.

TEST OF THE HYPOTHESIS

In order to test the AE hypothesis a search for data on rates of decay in forests of many climatic regions was undertaken. Few data of sufficient quality and duration to pursue the effects of climate in decay were discovered. Some good data were useless because the climatic variables required to compute AE were not published or gathered or the test site was distant from any weather stations. J. Van der Drift (1963) measured the accumulation and loss in dry weight of leaf litter in a mature deciduous forest near Autphen, Holland. He measured and reported the monthly precipitation and temperature from which we may compute AE according to Thornthwaite's method (Thornthwaite and Mather, 1955).

Figure 1 presents a simple regression of the percentage of decomposition measured by Van der Drift for forest litter with the annual Actual

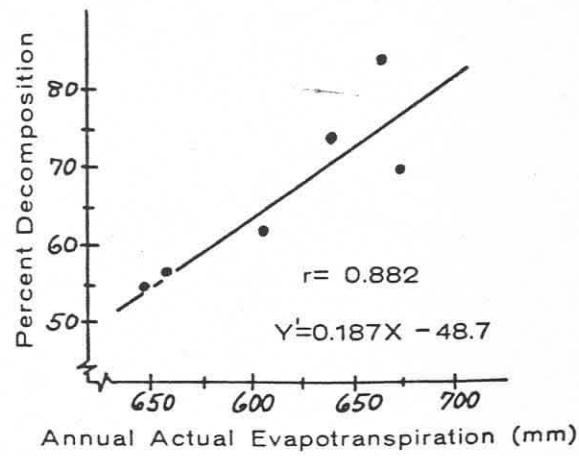

Fig. 1 Regression of actual evapotranspiration against percentage of material decomposed in a temperate forest.

Evapotranspiration. The correlation coefficient in Fig. 1 is moderately high with r = 0.88, significant at 0.05. There is a fair relationship in spite of the severe problems of measuring accurately the loss in dry weight *in situ*. However to avoid spurious conclusions due to a small sample and an environment with limited annual variability of energy and moisture endowments, we must examine other forests.

Madge (1965) performed studies of decomposition rates and decomposer activity in a tropical forest near Ibadan, Nigeria, in which he attempted to demonstrate the relationship of the weather with the decomposition rate of leaf litter. From his published data we computed Actual Evapotranspiration in order to further analyze its relationship with measured decay rates.

Figure 2 demonstrates a regression of the monthly AE at Ibadan against the monthly percentage of litter decomposed. The coefficient of correlation in Fig. 2 is again moderately high with r = 0.89, significant at 0.01. The data used in Fig. 2 were derived from a tropical, wet-dry forest. The data are monthly whereas they are yearly in the previous example for Autphen, Netherlands. Actual Evapotranspiration apparently possesses a strong relationship with measured decomposition for monthly intervals as well as for yearly intervals and consequently may be used to predict the decay rate in environments where there is a seasonally dry period as well as in environments that are rather constantly humid.

Figure 3 demonstrates the seasonality of decay at Ibadan and presents a comparison of the predicted decay with that actually measured by Madge. It also demonstrates that Actual Evapotranspiration is a rather precise predictor of decay. Although precipitation virtually ceases after

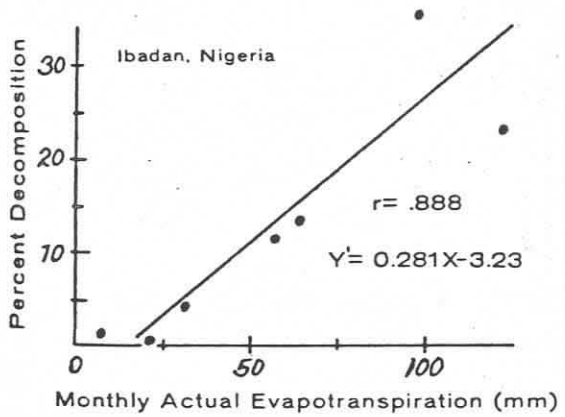

Fig. 2 Regression of monthly actual evapotranspiration against the monthly percentage of leaf litter decomposed in a Nigerian forest.

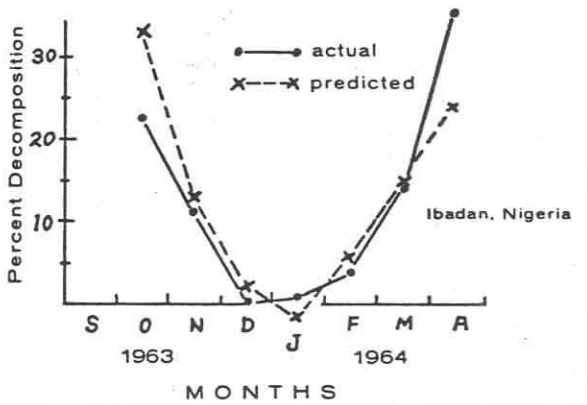

Fig. 3 Seasonal trends in predicted rate of decomposition of leaf discs compared to the measured decomposition rate in a Nigerian forest.

September at Ibadan, decay rate does not cease when the rains cease. Free film moisture is still available in soil and litter. because of moisture storage capabilities. Not until December is this stored moisture depleted, the value of AE reduced to almost zero and the decay process halted. Measures of the weather, such as temperature and precipitation, are often inadequate as predictors of decay rate because they do not account for the possible storages of capillary water in the soil and litter.

Some secondary mechanisms of decay rate also are demonstrated in Fig. 3. The overestimation of decay rate in October and its underestimation in April probably is caused by successional aspects of microorganisms attacking a new versus an old substrate. When new litter is produced the microorganisms rapidly attack their food and their productivity is high. On an old substrate the microorganisms display the typical properties of mature ecosystems in which there is considerable diversity and stability but a lower productivity and hence a lower rate of consumption of the substrate.

At Ibadan the AE relationship is verified at least tentatively for dry environments as well as cool, temperature environments, and for monthly decay rates as well as annual rates. The previous examples have employed decay of leaf litter. Decay of humus portions of organic debris in forests has not been examined. However, as is demonstrated in the following example, AE also should relate well with the decomposition of all organic matter in the litter/soil system.

Reiners (1968) measured for an entire year the evolution of carbon dioxide from the forest floor of an oak forest in east central Minnesota. Carbon dioxide production is presumably a good measure of decomposition rate because it accounts for all of the metabolism of decomposer organisms. From

data which Reiners kindly supplied to the author it is possible to compute the monthly evolution of carbon dioxide and the monthly AE, and to compute the regression between the two.

Figure 4 demonstrates the relationship between evolution of carbon dioxide and monthly AE. Again there is a close linear relationship as indicated by a coefficient of correlation with r = 0.92. The AE hypothesis is confirmed by these data for the permutations of hot and cold, and relatively moist conditions encountered in Minnesota. A strong statistical relationship of AE to measured decay rates is confirmed. Although it may be sufficient merely to demonstrate that AE is a measure of the forcing function by energy and moisture in decomposition, a model, even a preliminary model would be desirable in order to facilitate further experimentation and application to existing data.

A CLIMATIC MODEL OF DECAY

All of the previous demonstrations of the relationship of AE with decay rates have been derived from decay data resulting from differing measurement techniques and differing time intervals of measurement. Therefore a search for data from differing environments but with similar measurement procedures and similar time intervals (monthly, yearly, etc.) was undertaken. Data from Van der Drift (1963) and from Mikola (1960) in Finland were selected as appropriate for curve fitting and representation as a preliminary model. Ten observations resulted from the combination of these data.

Figure 5 demonstrates a regression model using the combined data which may be used to predict

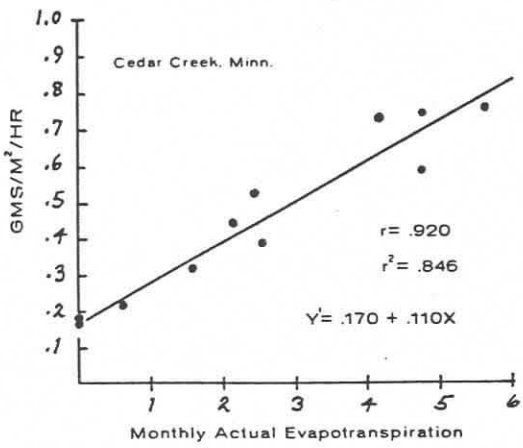

Fig. 4 Plot of monthly actual evapotranspiration against the mean monthly evolution of carbon dioxide from the forest floor of an oak forest in East Central Minnesota.

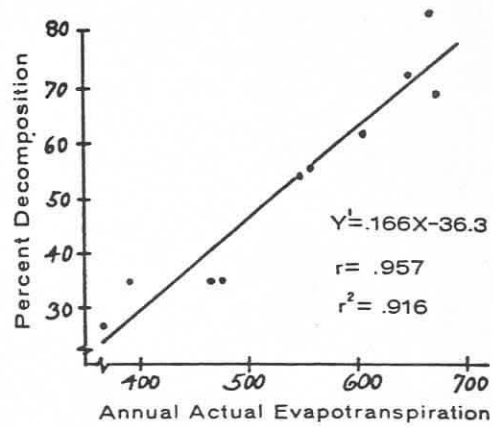

Fig. 5 Regression model of decomposition rate. Actual evapotranspiration (annual in mm) is plotted against annual percentage of litter material lost.

the annual percentage of leaf litter which will decay in forests. Annual AE is the predictor and accounts for about 92 percent of the variation in the observed decomposition rates. However one should expect to find significant local variations in decay rate because of non-climatic effects. Furthermore the curve-fit does not include data from the tropics. Yet if the regression line is extended to indicate some AE values occurring in the humid tropics (AE in excess of 1500 mm), then according to the curve-fit model the decomposition of litter should be several times faster than the litter produced. This correlates well with reports that decay rates in the humid tropics may be as much as four times faster than the rates of litter production.

An application of the curve-fit model to the Eastern United States is presented as Fig. 6. The 100 percent line is of interest because it suggests that the annual leaf fall and annual decay rate for leaf litter should be equal along that line. It corresponds approximately with those places with

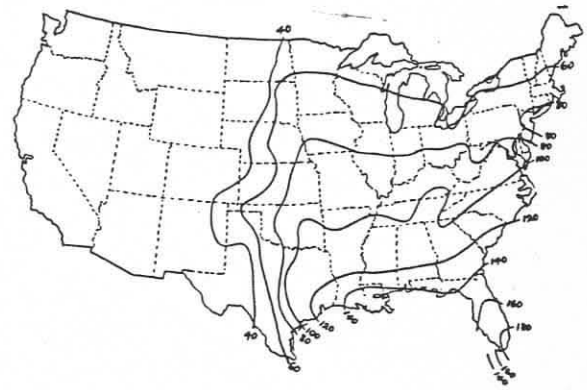

Fig. 6 Prediction of the regional percentage of average annual leaf production which can be decomposed within 12 months.

an annual AE of 850 mm. Decay rates less than 100 percent will yield an annual "holdover" of material while places with a decay rate greater than 100 percent will have little or no "holdover." The pattern in Fig. 6 fits our qualitative knowledge of decay rates, but more significant perhaps is the pattern's apparent relationship with the geography of soils in the Eastern United States.

Admittedly all data in this preliminary study have been derived from published sources and while the regression model in Fig. 5 applies in a strict sense to leaf litters only, the possibility of applying it in studies of soil formation is tempting. It is likewise tempting to apply the model's concept, if not the model itself, to those organic products of human origin deposited on the earth's surface. In spite of the inadequacies of the model as presented, it is a proposition that possessess a simple elegance and a largely unknown utility. It is possibly the first model to resolve the simultaneous controls of energy and moisture on decomposition by organisms.

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